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Some applications of the quadrat method

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By the quadrat method in ecological phytogeography is meant the intensive study of the vegetation or environment of a limited and definitely circumscribed area, known as a quadrat, in order to gain a comprehensive knowledge of the vegetation as a whole. The development of the method is the direct outgrowth of a need which has been felt by every ecologist who has seriously attempted the study of vegetational units. While its use is of great value and leads frequently to generalizations which would otherwise be difficult or impossible, it is not complete in itself, and ecologists are unable to rely upon it alone as a means toward successful field work. Indeed, its use to the exclusion of all other methods has never been suggested. It does constitute, however, the only practicable means for the quantitative study of the association, and as such it forms an important adjunct to photography and verbal description, which were previously the only feasible means of presenting the structure of vegetation. It also plays an important part in the study of associational dynamics, as migration and succession, and environometry.

It is exceedingly difficult and in many cases impossible for a reader to form a clear mental picture of an association from a written description, as may be demonstrated by a perusal of any discussion of an otherwise unfamiliar type of vegetation. The value of a verbal description is always greatly enhanced by photography. There are certain physical limitations to the value of a general photograph, caused by the difficulties of field photography and the necessity of reducing the print to the usual compass of a page, so that a general view of an association seldom gives a sufficiently clear idea of the vegetation, since the component species are distinguishable only in the immediate foreground, if at all. A detailed photograph of a small part of the association, on the other hand, is frequently made with difficulty and it is often impossible to choose for illustration an isolated portion which is

typical of the association as a whole. In the latter case, and in all cases of verbal description, the result unconsciously and unavoidably embodies the author's idea of the conditions, rather than the actual and impersonal facts, in that conspicuous species may be emphasized although possibly relatively unimportant, while important but comparatively inconspicuous species may be neglected. While the quadrat method is by no means a panacea for all these difficulties, its proper combination with verbal description and photography does much to aid the observer in securing a thorough knowledge of the association and in more satisfactorily expressing its structure in terms intelligible to his readers. The merit of the method lies not merely in the actual results which it affords but also in the deductions from and application of these results.

While quadrats may be of any chosen size, a single square meter is probably most frequently used. In the list quadrat, a simple list is prepared of the species included within it. In the count quadrat, the number of individuals of each species is also determined. Both of these are of value as a method, but are of little use in expressing results. For the latter purpose, the map quadrat is by far the most useful. A chart is prepared on a suitable scale, usually 1 to 10, and the location of each individual plant noted upon it. Other sorts of quadrats may be made for special purposes, concerning which reference may be made to the various works by Clements (1904, 1905).

The structure of a vegetational unit depends upon the species represented, determining the flora; on the relative number of individuals of each, determining by their form, size, and habit the appearance of the vegetation; and on the total number of individuals, determining the density of the vegetation.

The use of a chosen quadrat in representing this structure depends absolutely on the theory of the homogeneity of the association, which in turn depends on a number of factors (Gleason, 1917, p. 471). Given a uniform physical environment, the mere migration of some species over the whole area requires considerable time and interferes with the uniformity until it is accomplished, so that young associations are always less uniform than old ones, while in open associations migration may continue for a

very long period. Minor differences in environment may lead to the predominance of certain species in favorable places, to the persistence of relics, or to the early appearance of pioneers of other associations. Uniformity can not be perfect, although the general tendency of vegetation (apart from the effect of disturbing physical factors) is always toward uniformity, and it is most nearly attained in old (climax) closed associations, where entrance of new species is prevented by vegetative control of the environment, or in associations of extreme environment, where a small group of adjusted species enjoy a monopoly of the area.

If the association were absolutely homogeneous, if the plant individuals of the different component species were as regularly distributed as water and alcohol in a mixture of the two liquids, all quadrats of appreciable size would be similar and any quadrat could be chosen to represent the vegetation. Since no association is perfectly uniform, any one quadrat may by its structure accentuate the variability instead of concealing it. The value of a single quadrat also depends on its size and on the number of species in the association. In communities of numerous species (75 or more), a meter quadrat seldom includes as many as fifteen of them and usually contains still fewer. In very open associations, a meter quadrat frequently includes but a single individual plant. In either case, the error is reduced by increasing the size of the quadrat, but this simultaneously increases the labor of charting and decreases the value of a photograph.

The single quadrat of small size, one to two meters square, is therefore essential for graphic illustration, either by photograph or map, and is undoubtedly of value also for experimental work, but it fails to give a fair representation of the whole association, and is of less value as a basis for written description or as a unit for intensive study in field work. To be sure, a suitable quadrat may be chosen, but the quadrat method itself, as ordinarily used, offers no aid in the selection of this typical area, so the actual choice invariably represents the observer's idea rather than the impersonal facts.

The chief value of the quadrat method lies in the results obtained from the study of many quadrats, chosen at random to avoid the personal element, scattered over an area wide enough

to be representative of the whole association, of sufficient number to permit drawing logical conclusions, and of a size suitable to the character of the vegetation concerned. Several ecologists have devised statistical methods toward this end, which have been more or less successful. One of the earliest was Drude (1890), who described plants as social, gregarious, copious, or rare, depending on their number, their distribution, and their grouping. He also proposed the determination of the frequence of plants on a large scale by dividing an area into quadrats of 100 square kilometers. Pound and Clements (1898, 1900) adopted the same terminology in their first studies on the subject, but determined abundance within a single association by actual counts of the number of individuals in a quadrat 5 meters square, and investigated enough quadrats to warrant them in drawing averages. It is obvious, however, that averages from figures obtained in this way are not entirely trustworthy, since some species are mutually exclusive, while the averages might indicate that they normally grew together. Jaccard (1901) adopted the study of several adjacent quadrats as a method in his study of alpine vegetation, and developed the idea of the frequency index and the community coefficient. His results are, however, probably somewhat faulty, inasmuch as he used few quadrats in any one association and located them adjacent to one another. Harper (1917 and several other articles) has also attempted a statistical expression of car-window observations, which corresponds to some extent to the frequency index as here used. Raunkiaer (1909) used essentially the same method described here.

The present writer first attempted the use of statistical methods to determine and express the structure of vegetation in 1903 (1907). He improved his method somewhat in 1908 (1910) and adapted it to class work with students in 1910. In the summer of 1911 he began the intensive study of the quadrat method and its applications at the Biological Station of the University of Michigan, and during the following four summers obtained a long series of data upon which the present paper is based. The statistics used in TABLES I and II were secured from the aspen (*Populus tremuloides* and *P. grandidentata*) association.

In practice, the following method is adopted. The size of the

quadrat to be used is determined first by the general character of the vegetation, using a small one, one square meter, for dense closed vegetation, and a larger one, two meters square, for open or irregular associations. The quadrats may be marked out by four stakes connected by a line of proper length, or they may be estimated by the eye with sufficient accuracy for all practical use. The optimum size can be ascertained after an examination of the preliminary results, and the survey can be repeated with a better size of quadrat if the first is unsatisfactory. The number to be counted depends upon the visible uniformity of the association, on the area covered by it and on the time available. If possible, one hundred are counted.

The first one is located anywhere. The others are located successively in a pre-decided relation to the first, thereby obviating any element of personal choice. Thus they may be in a straight line and separated by ten paces each, so that the whole strip of one hundred would be one kilometer long; or they may be in a square, but similarly separated, so that the area examined would be approximately 100 meters square; or any other arrangement of separate or contiguous quadrats may be used, depending upon the configuration of the association.

For the first quadrat, the species are listed and the figure 1 placed after each in a single vertical row. For the second, the figure 2 is placed after the 1 for all those species which occur also in the second quadrat, and new names followed by the figure 2 are added for the additional species. The process is continued to completion, when it is seen that some of the species occur in a majority of the quadrats and others in a few or only in one, and the common species are distinguished from the rare ones as the work proceeds.

At the conclusion of the count, the results are summarized and the ratio between the total number of quadrats and the number in which a particular species occurs is expressed as a percentage which is known as the *frequency index*, here abbreviated to *FI*. Thus, the frequency index of a common species may be as high as 100 and most associations show certain species with *FI* 90 or more, while others are as low as 1.

Obviously not every species of the association will appear in

the counts. Some of the rarer ones will be missed completely. For example, during five years experience in the aspen association of northern Michigan, during which some thousands of quadrats have been counted by the writer or his students, *Cypripedium acaule*, a plant of great rarity in this habitat, has appeared but once in the quadrats. These rarer ones, while of the greatest interest to the systematist or the phytogeographer in their relation to plant distribution in general, as emphasized so interestingly by Fernald (1919), and to the ecologist through the evidence which they frequently offer concerning the past or future development of the association, are nevertheless of negligible value in formulating a verbal description of the association. But the important species all do occur, provided the number and location of the quadrats has been properly chosen with reference to the size and character of the association, as the writer has demonstrated frequently in his own work.

If the whole association were included in a single quadrat, the frequency index of each species would be 100 and would give no idea of the comparative value of the species. In general, if the quadrats are too large, the frequency indices are also large and tend to approximate near 100. Conversely, if they are too small the indices are also small, and tend to approximate near unity, while the number of omitted species tends to become large and may even include some of the more important ones. The optimum size is one in which there is a wide divergence in the indices, from 1 to 90 or even more, so that the variation is an indication of the relative importance of the species. This is illustrated in the first three columns of figures in TABLE I,* of which the second column, based on quadrats two meters square, presents probably the best series of indices.

* The frequency indices given in TABLE I are not considered typical of the aspen associationi n general. The association consists of a sparse growth of two species of aspen and the paper birch, alternating with treeless areas dominated by bracken fern. The 240 quadrats counted for this paper were located entirely within a treeless area, and do not take account of the conspicuous difference encountered in the shade, where *Melampyrum lineare* and *Diervilla Lonicera* are both abundant. Neither do they cover an extent wide enough to give a fair representation of the treeless areas in general, since these omit completely such relatively common species as *Vaccinium canadense*, *Panicum depauperatum*, *Oryzopsis pungens*, and *Convolvulus spithamaeus*.

Again, the number of quadrats counted determines the accuracy of the frequency index as an expression of the ecological value of each species. The results from a small series certainly can not express the actual conditions as well as those from a large

TABLE I

	F/ in 15 quadrats of 16 square meters	*F*/ in 60 quadrats of 4 square meters	*F*/ in 240 quadrats of 1 square meter	*F*/ in every fourth quadrat	*F*/ in first 60 quadrats	*F*/ in second 60 quadrats	*F*/ in third 60 quadrats	*F*/ in fourth 60 quadrats
Pteris aquilina	100	100	99	100	98	100	97	100
Vaccinium pennsylvanicum	100	82	71	70	82	78	97	27
Gaylussacia baccata	80	67	48	43	60	25	87	22
Aster laevis	100	68	29	30	37	30	23	27
Carex umbellata	87	53	24	33	57	20	7	13
Rhus glabra	73	55	23	25	33	15	3	40
Rumex Acetosella	80	40	21	28	7	33	33	12
Rubus allegheniensis	40	30	17	18	37	15	10	7
Panicum boreale	60	35	16	17	5	12	17	32
Danthonia spicata	40	22	15	13	2	48	3	7
Gaultheria procumbens	47	27	14	10	7	20	25	5
Gnaphalium decurrens	60	33	12	15	2	20	17	8
Populus grandidentata	53	32	11	10	0	10	8	25
Hieracium venosum	60	28	8	7	3	7	5	18
Erigeron canadensis	33	20	7	8	5	0	2	22
Panicum xanthophysum	20	13	6	3	0	2	0	23
Diervilla Lonicera	13	8	4	3	15	0	0	0
Solidago canadensis	33	8	2	2	2	0	3	5
Agrostis hyemalis	27	8	2	3	7	2	0	0
Lactuca canadensis	20	7	2	2	3	0	2	2
Poa compressa	13	5	1	2	2	3	0	0
Epigaea repens	20	5	1	0	0	0	3	2
Quercus rubra	13	3	1	3	2	0	2	0
Comandra umbellata	7	2	1	2	0	3	0	0
Amelanchier canadensis	7	2	0	0	0	2	0	0
Hieracium paniculatum	7	2	0	2	0	0	2	0
Pinus resinosa	7	2	0	0	0	0	0	2

series. Repeated tests have shown that 100 is a satisfactory number and that no valuable increase in accuracy is gained by increasing the number beyond that, while it eliminates all computation in determining the frequency index.

Experience has also shown that better results are obtained if the quadrats are not contiguous, but separated by some distance, so as to cover more thoroughly the whole area of the association. In small associations, where even contiguous quadrats cover most of the area, this treatment is not necessary. If plants were

distributed absolutely at random over the association, that is, if the association were absolutely uniform throughout, separated quadrats would never be necessary. But plants are not distributed entirely at random. Each plant-parent gives rise to disseminules which occupy, roughly speaking, a circle about it, with a diameter depending upon the mobility of the disseminules. As early as 1903 the writer (1907, p. 159) was able to demonstrate these in his field work. As a check, the following data from 240 one-meter quadrats are offered. The 27 species have frequency indices ranging from 0 (1 quadrat only) to 99, based upon the whole series. If any fourth part of the series is taken as a basis, composed of 60 contiguous quadrats, as shown in the last four columns of TABLE I, the average discrepancy between the two series of indices is 6.8, or for the 15 commonest species 10.7, and the difference may be as high as 44 for a species which normally grows in patches. But if every fourth quadrat is taken as a basis, that is, 60 separated quadrats, as shown in column 4 of TABLE I, the greatest discrepancy is only 9 and the average only 1.9, or 2.7 for the commonest species. In other words, 60 quadrats well scattered give results practically as reliable as 240 contiguous ones.

From a list of the frequency indices, made from quadrats of suitable size and number, the species are arranged in order of their general distribution in the association, and any number of them may be segregated for further study as the most typical or commonest. Since the frequency index increases with the size of the quadrat, a quadrat of proper size may now be chosen which will normally include all the more important species as well as a number of the less important ones also. The size of this *major quadrat* may be determined in advance and, in field work with students, one of them assigned to each student for detailed study and description. Although every such major quadrat may not actually contain all the important species, the student may be assured that it is nevertheless a fair sample of the association as a whole. The value of setting a definite area before each student, in which he may do his more intensive work, will be at once apparent to every teacher who has tried to present this phase of ecology in the field. The method of determining the major quadrat will be discussed below.

The relative abundance of a species is a fair measure of its ability to maintain itself under the conditions of environment and competition prevalent within the association. Long-established species of an old association have frequently become diffused thoroughly over the whole area, and their abundance may be determined by counting, but recent immigrants into old associations or any species of young associations are not uniformly distributed. The number of individuals of such plants is therefore zero in those parts which they have not yet reached and is too high to show their relative adjustment in those parts which they have reached.

But there is a definite relation between the number of individuals of a species and its frequency index. If only one is present in the area covered by the quadrats, the frequency index naturally cannot exceed 1. If only two are present, it can not exceed 2 and may be only 1 if both happen to occur in the same quadrat. While it is possible for a species to be represented by a large number of individuals all of which occur in a single quadrat only, the chance of such a thing actually happening is very small indeed. Similarly, while 100 individuals might be so thoroughly distributed that they would occur one in each quadrat, there is again very slight probability of it. The mathematical possibilities are capable of solution according to the laws of probability and chance. If n plants are scattered at random over q quadrats, the probability of any one quadrat being occupied is expressed by the formula $1 - \left(1 - \frac{1}{q}\right)^n$. Thus for 2 plants in 5 quadrats $1 - \left(1 - \frac{1}{5}\right)^2 = 0.36 = FI\ 36$. Or for 65 plants in 100 quadrats $1 - \left(1 - \frac{1}{100}\right)^{6/5} = FI\ 48$. Or, conversely, $FI\ 48$ should indicate a total of 65 individuals within the 100 quadrats. But since plants are not distributed entirely at random, the actual number is therefore always greater than indicated by the mathematical formula, which may be expressed, when $q = 100$, as $n = \frac{\log\ (1 - FI)}{\log\ 0.99}$. Thus, *Pteris aquilina*, determined by actual count to have an average abundance of 4,400 in 100 quadrats, has $FI\ 99$, corresponding to a theoretical number of only 455 individuals. Obviously, the

discrepancy between actual and theoretical number should be, and is, greatest in species of high frequency, *FI* 95 or more. It is not possible to draw any accurate conclusions as to the relation between theoretical and actual number of individuals, but in general, the theoretical number is one fifth to two thirds as large as the actual, and results any more accurate than this are probably of little or no value in ecological description.

The determination of the proper size of the major quadrat involves reducing the original series of quadrats to a smaller number of larger quadrats, thereby increasing the frequency index of selected species to 99 or more. With *FI* 99 or more for all the important species, it may be assumed that this quadrat is large enough to serve as a fair sample of the association.

In the original equation $1 - \left(1 - \frac{1}{q}\right)^n = FI$, substitute for q the number of quadrats actually counted, use for *FI* the index of the least common one of the important species, and solve for n. Substitute again the determined value for n and 99 for the original *FI* and solve for q. The equation is $1 - \frac{1}{q} = \sqrt[n]{.01}$ (presuming 100 quadrats were counted), from which q may be easily determined. For example, in a certain association, it is desired to determine a major quadrat which will probably contain all the species with *FI* 60 or more.

$$1 - \left(1 - \frac{1}{100}\right)^n = 60\text{: } n = 90$$

$$1 - \frac{1}{q} = \sqrt[90]{.01}\text{: } q = 20 \text{ (fractions omitted)}$$

That is, the original 100 quadrats redivided into 20 larger quadrats should show *FI* 99 or 100 for all species which originally had *FI* 60 or more; or the major quadrat should be five times as large as the original. The error concerned in computing the value of n, due to imperfect distribution of the species, does not affect this last equation, and experience has shown that it gives surprisingly good results. On the average, four major quadrats out of five, the location of which is chosen at random, present all the important species for which they were computed.

Jaccard's *community coefficient* (*CC*) was designed to express by a number the degree of similarity between two areas of vegetation. His method is to divide the total number of species in both areas into the number common to both. Thus, two areas, each containing 30 species, of which 20 were common to the two, contain a total of 40 species, and the community coefficient is accordingly 50. Jaccard's method fails to take account of the much greater importance of some abundant species, and the resulting error of computation may be obviated, in part at least, by weighting each species with its frequency index. Referring to columns 5 and 6 of TABLE I, and weighting each species with its average index in both columns, the results, shown in TABLE II

TABLE II

	In first area only	Common to both areas	In second area only
Pteris aquilina		99	
Vaccinium pennsylvanicum		80	
Gaylussacia baccata		42.5	
Aster laevis		33.5	
Carex umbellata		38.5	
Rhus glabra		24	
Rumex Acetosella		20	
Rubus allegheniensis		26	
Panicum boreale		8.5	
Danthonia spicata		25	
Gaultheria procumbens		13.5	
Gnaphalium decurrens		11	
Populus grandidentata			5
Hieracium venosum		5	
Erigeron canadensis	2.5		
Panicum xanthophysum			1
Diervilla Lonicera	7.5		
Solidago canadensis	1		
Agrostis hyemalis		4.5	
Lactuca canadensis	1.5		
Poa compressa		2.5	
Quercus rubra	1		
Comandra umbellata			1.5
Amelanchier canadensis			1
	13.5	433.5	8.5

are obtained, from which the community coefficient of the two areas concerned is determined as 95, by dividing the sum of the three columns, 455.5, into the sum of the center column.

By Jaccard's method, giving equal weight to each species, 24 total species divided into 15 common species = *CC* 62.

This method, while doubtless better than the original one, is still deficient in allowing equal weight to such small slender plants as *Erigeron canadensis* and large bushy ones as *Gaylussacia baccata*. If each plant could be further weighted by a multiplier expressive of its size, a better index would doubtless be attained. In this particular case, for example, each plant of the latter species occupies probably 400 times as much ground space as the former. So far no serious attempt has been made to follow out this suggestion.

It is freely admitted that the expression "*FI* 55" means little to a person who has not already experienced its meaning by actual field work. But to such persons it does present at once an idea of the relative abundance of that particular species, and an idea much more accurate than any such general expression as *common*, *rare*, or *copious*. Students who have used the method adopt it into their scientific vocabulary and actually use it in their conversation, almost as freely as they refer to degrees of temperature. The writer has heard a student, describing the luxuriant growth of *Epilobium angustifolium* following a recent fire, state that it must have had "a frequency index at least 90," instead of resorting to the usual hyperbole to express great abundance, or, in alluding to a new station for a *Habenaria*, say "There was a good deal of it all through the woods: *FI* probably 5 or 10." And if such a student should read an account of an utterly unfamiliar vegetation in some remote part of the world, in which the frequency indices were given, he would at once have a relatively clear idea of the actual conditions.

Nevertheless, the quantitative study and description of vegetation are still in their infancy, and there is every opportunity for great improvement.

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